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Soil Chemical Factors and Biological Activity

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Biological activity is chemical in nature and is strongly affected by the chemistry of the microhabitat in which organisms exist. In the present discussion we shall consider the chemical environment as varying and the organism's chemistry as fixed. This assumption is made for simplicity of discussion and not out of any non-Darwinian adherence to "fixed species" concepts.

The subject at hand could be approached by considering biological processes and describing those chemical factors of soil which have been found to influence them, or, conversely, by describing the influences of chemical factors of soil on the physiological processes and ecological activities of soil organisms. The latter approach has been found somewhat more adaptable to the present discussion. For convenience, the soil factors are generally divided into inorganic and organic categories. The chemical environment of the soil in relation to plant growth and diseases was reviewed by Chapman (8).

INORGANIC FACTORS.—*Water.*—Both intracellular and extracellular chemical reactions take place principally in water. Thus, a knowledge of the properties of water, and how these may affect biological systems, is essential for understanding how the chemical environment may influence the activities of the soil flora and fauna.

Water as it occurs near soil particles is somewhat unique in that it differs in several respects from "normal" liquid water. These differences are due to the adsorption of water on clay mineral surfaces, which results in an increased orderliness of its molecular structure. This enhanced structure, which may be termed quasi-crystalline, close to clay surfaces results in a lower potential energy and greater viscosity of the adsorbed water as compared with free water (38). Oxygen and CO_2 are less soluble and diffuse more slowly in adsorbed than in free water. These conditions might result in low O_2 concentrations in microhabitats where one would not expect them. This would offer at least a partial explanation of how obligate anaerobes function in apparently well-aerated soil. Low (38) has suggested that adsorbed water is less available to organisms than free water. Also, the freezing point of quasi-crystalline, adsorbed water is depressed. This may provide a water pool at subfreezing temperatures. Weathering of minerals may proceed under these conditions; thus, the soil solution is continuously recharged with nutrients essential for microbial growth.

The diffusion coefficients of all ions are reduced as a consequence of the enhanced water structure. The anions, however, farther from the negatively charged clay mineral surfaces, are surrounded by less viscous water than the cations, and therefore are affected less.

The thickness of the ordered water is limited, but so is the over-all thickness of the water films around soil particles. An illustration of this point was offered by Rapoport and Tschapek (59) who stated, "Even soil bacteria spend the greatest part of their lives in a way that can be roughly defined as an 'almost permanent foot bath.'"

Not only is the structure of water altered by adsorption by colloids and by the obvious changes associated with changes in state, but there also appear to be more subtle within-state changes that may have importance in biological systems. These so-called higher-order phase transitions occur rather abruptly in liquid water at four biologically important temperatures: 15, 30, 45, and 60 C (all ± 2 C). This subject was summarized by Drost-Hansen (17) at a symposium on forms of water in biological systems. More recently, Davey et al. (14) showed a suppression in the growth of bacteria in aqueous culture at each of the four temperatures.

Shapiro (69) inadvertently demonstrated water structure-induced discontinuities while studying the effects of temperature on the rates of P uptake and release by microorganisms. There was a pronounced depression in the rates at 15 C. Several studies discussed by Drost-Hansen (17), as well as the more recent studies mentioned above, suggest a strong interaction between the structure of water and biological activity. Much research is needed to elucidate the role of the higher-order phase transition changes in water structure in the soil where the ordering effect of the clay mineral surfaces exists.

Acidity.—The soil acidity (pH) has long been recognized as an important characteristic which influences biological activity. Acidity in the soil may be a result of H-ions in the soil solution or a combination of H- and Al-ions. Since the H-ion, in concentrations normally encountered in the soil, is not toxic, and the Al-ion is toxic at fairly low concentrations, the possibility exists that two soils with the same pH may exercise quite different acid-dependent effects on biological processes.

The effect of Al added to soil on microbial processes was reported by Mutatkar (44), and by Mutatkar and Pritchett (45, 46), in acid tropical and subtropical soils. They found that the decomposition of organic matter increased as acidity decreased. In these naturally acid soils, added Al had little effect on microbial activity above pH 4.5, even though additions of Al below this value markedly reduced activity. Some plants tend to accumulate large amounts of Al, and this may influence the rate of their eventual decomposition in soil.

The ecological role of Al in biological processes in soil has not been investigated sufficiently. This appears to be a fruitful area for investigation.

Even though Al ceases to be a significant factor at or above pH 5, soil acidity still has a significant effect on microbial activity. In the decomposition of plant residues, two major factors may be involved: effects on decomposition rates and changes in the specific organisms involved in the decomposition process. Went and DeJong (86) concluded that acidity was not a major determining factor in the rate of breakdown of introduced cellulose in mull and mor soils. However, the types of organisms attacking cellulose in the soil were strongly influenced by acidity. Dubos (18) reported that only under optimum conditions, including a neutral or alkaline soil reaction, would bacteria play as large a role as fungi in cellulose decomposition. Likewise, Szegi (78) reported that actinomycetes have a narrow ecological niche in terms of cellulose decomposition in soil. Only within the range of pH 6-7 were they capable of attacking cellulose, even though they could grow in soil over a much wider pH range if provided with glucose as an energy source.

The occurrence and distribution of the Saprolegniaceae in relation to soil pH and moisture content was studied by Dick (15). He found that neither the distribution by family nor by genera could be predicted by a single parameter. He concluded that it is necessary to define habitat preference at the species level.

In addition to affecting the activities of individual organisms, soil acidity may also influence the composition of the entire microbial population. Kaufman and Williams (31) found that differences in acidity between pH 4.5 and pH 7.5 did not affect the total number of fungi in the soil but significantly changed the species composition.

Taylor and Parkinson (79) determined that acidity was a significant factor in the colonization of bean roots by fungi. *Trichoderma viride* Pers. ex Fr. and *Penicillium* species predominated on the roots under highly acidic conditions but decreased markedly as acidity decreased. *Cylindrocarpon radicicola* Wr. behaved in the opposite manner, and several species of *Fusarium* each reacted differently to acidity in regard to root colonization. Emmatty and Green (19) discovered that acidity may alter the effectiveness of amino acids in reversing mycostasis. Working with *Trichoderma viride,* they found that certain amino acids were much more effective in breaking mycostasis in an acid environment than in a less acid system. Thus, in light of Emmatty and Green's work, one might expect that in the rhizosphere stimulation of a specific organism might be due to the annulment of mycostasis by the acid nature of the environment. This effect would be in addition to the effect of organic nutrients supplied from roots.

Bateman (5) demonstrated that saprophytic and parasitic activities of *Thielaviopsis basicola* (Berk. & Br.) Ferr. may be affected differently by acidity, and that the effect of soil acidity on disease development probably is indirect. He found that saprophytic growth in culture was greatest in the range of pH 4.7-5.5. Growth was reduced markedly at or above pH 7. In nonsterile soil, however, both bean and poinsettia were not diseased below pH 5.5, while their root systems were destroyed within 2 weeks in neutral or alkaline soil. When the normal soil flora was eliminated, beans were found equally susceptible from pH 4.7 to 8. After addition of inoculum to nonsterile soil, at pH 4.7 and in the absence of a host, over 90% of the added inoculum was undetectable within 1 month, while it was essentially all detectable in soil at pH 8. After soil is infested with endoconidia of *T. basicola,* there is a rapid inoculum stabilization (49). Survival of the endoconidia is enhanced in neutral or alkaline soil.

The influence of soil acidity on the activity of parasitic organisms is often complex. For example, when soil supporting loblolly pine seedlings was limed to pH 7.5, the trees became chlorotic and nearly nonmycorrhizal. Soil iron was unavailable under these near-neutral conditions, and this resulted in chlorosis and the production of little photosynthate, which in turn was responsible for the inability of the mycorrhizal fungi to colonize the roots. A foliar application of chelated iron corrected the chlorosis, increased photosynthetic efficiency of the trees, and permitted normal mycorrhizal development without changing the soil acidity.

High alkalinity in soil also has a strong influence on biological activity. Applications of ammonia, sufficient to cause the soil to exceed pH 9.8 for a period of 24 hr, killed sclerotia of *Sclerotium rolfsii* Sacc. (28). Since loss of viability of sclerotia occurred when they were exposed to solutions adjusted to pH 9.8 or higher, whether or not any ammonia was present, the authors concluded that the effect was caused by the high alkalinity rather than toxicity of ammonia.

The general nature of the soil microflora also may be completely altered in extremely alkaline soils. In a study of Indian soils (pH 7.7-11), Mukerji (43) found that the numbers of fungi were markedly reduced by increasing alkalinity. In the most alkaline soils, fungi were almost eliminated, whereas the bacterial numbers did not appear to be affected.

Not only is the absolute acidity an important factor in microbial physiology and ecology, but the stability of the soil acidity may also play an important role. Soils with a low content of mineral or humic colloids have a low buffering capacity, and as a consequence the pH of such soils fluctuates markedly. Stotzky (76) recently studied the influence of clay minerals on the respiration rates of bacteria in culture. He found that certain 2:1 type clays (e.g., montmorillonite and vermiculite) stimulated respiration while other 2:1 type clays (e.g., pyrophyllite and vermiculite-mica mixtures) and 1:1 type clays (kaolinite and halloysite) did not. Those clay minerals that stimulated respiration had a greater buffering capacity than those that did not, and they maintained the pH at a level suitable for sustained growth. The stimulation of respiration and the maintenance of favorable pH were related to the relative basicity of the exchangeable cations on the clays.

Cation exchange capacity.—The mineral and organic soil colloids possess varying numbers of negative charges. These charges attract and hold cations against leaching. However, such cations are not tightly bound to the colloids and hence may be readily exchanged by other cations. In soil this gives rise to the property known as cation exchange capacity (CEC), which has several important consequences. The CEC determines the amount of cationic nutrients that a soil can retain and serves as the reservoir of H-ions that are in equilibrium with the soil solution H-ions. Thus, the CEC is a major determiner of potential soil fertility, soil acidity (pH), and soil buffering capacity. These properties, in turn, influence many biological activities in the soil (76). The nitrification rate of NH_3 was shown to be reduced by reducing the soil CEC with sand (71). There were fewer cation exchange sites available for the $NH_4{}^+$, resulting in a decrease in soil solution acidity. With less ionization of NH_3, levels of NH_3 toxic to *Nitrobacter* accumulated and inhibited nitrification.

Organic as well as inorganic cations may be held on the exchange complex. Natural materials that may be adsorbed and affect microbial processes in the soil include substrates, exoenzymes, microbial metabolites, and plant residue degradation products. Thus, substrates such as amino acids and proteins; amylytic, cellulolytic, and proteolytic extracellular enzymes; and toxic or antibiotic metabolites might be removed from the soil solution and rendered less active or less available. The exact effect of adsorption of organic molecules will vary with both the nature of the adsorbent and the adsorbate. It has been shown that the adsorption of proteins on montmorillonite will reduce the rate of enzymatic hydrolysis, but protein adsorption on kaolinite may actually increase the rate of degradation by bacteria—presumably due to the concentrating effect of the charged clay surface (21, 22). This apparent contradiction probably is caused by interlayer and surface adsorption by montmorillonite and by surface-only adsorption by kaolinite. A more complete discussion on clay-organic complexes has been given by Greenland (23, 24).

Since the soil colloids are smaller than most of the soil organisms, which themselves possess surface charges, perhaps certain organisms adsorb some colloids. Lahav (35) studied the adsorption of sodium-saturated bentonite by different bacteria and found a wide range in the amount of clay adsorbed. The electrophoretic mobility of bacteria that adsorbed the clay was significantly reduced but was restorable on desorption of the clay colloids.

The cations adsorbed by colloids or organisms will depend on the composition of the soil solution. Rode and Foster (63, 64) recently reported that the germinability of bacterial spores was strongly influenced by the adsorbed cations. The germinability could be reversed by changing the saturating cation. They showed that the germinability of Ca-saturated spores could be reduced when H-saturated and reinstated when resaturated with Ca. The type of exchangeable cations on bacterial spores also have been shown to affect heat resistance (2), reversible restoration of dormancy (37), and spore germinability.

The effect of exchangeable cations held by organisms on biological activity offers a promising avenue for research in the near future. It would be interesting to know whether exchangeable cations maintain fungal spores, nematode eggs, and other resting bodies in a dormant stage under field conditions. If so, the possibility of purposefully varying the accompanying cations with anionic nutrients (phosphate and nitrate fertilizers) might be practical. This might have special appeal or practicability in the use of so-called "pop-up" fertilizers, which are applied directly with the seed at planting. For prevention of seedling maladies, the beneficial effect would not need to be of long duration.

Mineral nutrients and nitrogen.—This article is not intended to cover in detail the effects of nitrogen or mineral nutrition of the various types of microorganisms. The literature in this area is voluminous and deals mainly with pure culture studies conducted outside of the soil. Cochrane (12) listed nearly 900 references on this subject in his text on fungal physiology. Equally impressive numbers could be mentioned for bacteria, nematodes, etc. Consequently, in this section we will attempt to discuss only those aspects that have some direct bearing on the ecology of organisms in soil.

As previously mentioned, many of the cationic nutrients ($NH_4{}^+$, K^+, Ca^{++}, Mg^{++}, etc.) are held in the soil on the cation-exchange sites of the soil colloids. In soils other than structureless sands, many of the cation-exchange sites are located within soil crumbs and peds where access to nutrients may be limited. During soil genesis, clay films (called cutans) form on the outside of peds. Because cutans contain high proportions of very fine clay, they form tightly fitting coats on the peds. This limits access to internal cation-exchange sites. Plants had difficulty in obtaining K^+ from exchange sites located within artificial cutan-coated peds (73).

The influence of cutans on the activity of soil organisms appears worthy of investigation. There may be direct effects on the organisms that are caused by restricted nutrient availability, or there may be indirect effects on parasitic organisms resulting from the effects of the cutans on the nutrition of their hosts.

Man affects the chemistry of the soil profoundly by the addition of lime or fertilizer. The effect of fertilizers on soil organisms has resulted in several divergent reports. Prša (55) followed populations of organisms in a soil planted to corn throughout one growing season. He observed that mineral fertilizers sharply reduced the numbers of microorganisms, especially bacteria. On the other hand, Balloni and Materassi (4) reported that $NaNO_3$ and $Ca(H_2PO_4)_2$, added to soil supporting either peas or flax, increased the total number of bacteria, including the N-fixing bacteria. The microorganisms in the nonrhizosphere soil were affected more than the microflora of the rhizosphere. Joffe (30) found that the addition N, P, and K to a basic soil increased the total number of fungi, but it did not affect the number of species. These examples indicate that the effect of fertilizers on soil organisms will be strongly influenced by the state of the soil prior to fertilizer additions. The above work (4, 30, 55) was limited to a single growing season. Steinbrenner (75) reported on fertilization of an acidic soil with N, P, K, and Ca for 24 years. In the fertilized soil the numbers of bacteria and actinomycetes were markedly higher than in the nonfertilized soil; numbers of collembola and mites were increased slightly, and numbers of fungi were decreased.

Eno et al. (20) reported the influence of high rates of fertilization of Leon fine sand on celery yield and on composition of the soil microflora. They applied up to 5 tons of 5-5-8 fertilizer/acre (ca. 10,000 kg/ha) and observed that crop yields, soil respiration, nitrification, and numbers of bacteria decreased at fertilization rates above 3 tons/acre. They further determined that nitrification was reduced most by N and least by P.

Tyner (83) reported a rather spectacular stimulation of *Cephalosporium* in soil by the addition of lime. Previous to the addition of lime, this fungus was not detected. Three days after liming, dilution plates indicated a population of *Cephalosporium* of 1.2 million/g of soil. Such enhancement of fungus development might be of significance in biological control.

The influence of mineral fertilization and soil acidity on fungi antagonistic to four soil-borne plant pathogens was investigated by Kaufman and Williams (32). They reported that acidity, P, and K did not affect total soil fungi, but the numbers of antagonistic fungi increased as acidity decreased. Nitrogen, on the other hand, increased total fungi, but its effect on antagonists varied with the crop.

A high level of available N has been shown by several workers to be responsible for a depression of mycorrhizal development as a consequence of nearly complete utilization of carbohydrates by the host. Richards and Wilson (61) found that, as the level of N increased, the incidence of infection on Caribbean pine decreased. Lanowska (36) found that both *Rhizobium* infection of, and mycorrhizal formation on, pea roots was depressed by additions of NH_4NO_3. Also, Slankis (70) reported that high levels of nitrogen eliminated established mycorrhizae from roots of eastern white pine.

Trace, or minor, elements also influence biological activity in soil, but work with them has been limited. Kendrick (33) studied the soil microflora of swamps varying in Cu content. He found that fungi could be divided into three groups on the basis of Cu tolerance. One group included species that were isolated only from high-Cu-content swamps. The second was indifferent to Cu content, i.e., the fungi were isolated from both high- and low-Cu-content swamps. The third group included species that were apparently sensitive to the Cu concentration in that they were isolated only from swamps with a low Cu content. Thus, it appeared that a single soil chemical constituent determined the presence, or absence, of a large number of fungi. However, Cu may not have been the only difference among the swamps. Henderson (26) reported that Fe, but not Cu, Mn, or Zn, affected the rates of decomposition of several aromatic compounds by soil fungi.

Sadasivan (66) reported that B, Mn, and Zn were all effective in restricting saprophytic activity of *Fusarium udum* (Berk.) Wr. in soil, but only Mn controlled the wilt of red-gram that this pathogen incited. McGregor and Wilson (42) also found that Mn greatly reduced disease severity. They applied Mn to near-neutral soil and essentially controlled potato scab. According to Van Gundy and Martin (84), borderline deficiencies of Cu or Zn, as well as excess amounts of $CaCO_3$, Na, or K, increased susceptibility of sweet orange to *Tylenchulus semipenetrans* Cobb.

The chemical form, as well as the amount and distribution of a nutrient, influences biological activity in soil. Those nutrients that are capable of existing in different oxidation states fall primarily into this category. These include N, P, S, Fe, Mn, and Cu. By far the majority of the work reported in this area involves forms of N. Some work has been reported on forms of P but little or nothing on S or the trace elements. Many new forms of phosphates, including pyro-, poly-, meta-, and others, are being developed. Investigations on the effects of these fertilizer materials on soil organisms needs prompt attention.

The influence of the forms of N has been studied in terms of a range of microbial activities. However, we must recognize that other factors must vary when the form of N is changed. Cook and Schroth (13) reported that exogenous N and C are required in soil for germination of chlamydospores of *Fusarium solani* (Mart.) Appel & Wr. f. sp. *phaseoli* (Burk.) Snyd. & Hans.; NH_4+ was more effective than NO_3-. Toussoun et al. (81) studied conidia of *F. solani* f. sp. *phaseoli* from germination through saprophytic growth, penetration, and pathogenesis. They reported that exogenous N favors early penetration and pathogenesis and that reduced forms of N, in this case organic, were more effective than oxidized N as NO_3-. Papavizas et al. (50) found an increase in inoculum density of chlamydospores of *F. solani* f. sp. *phaseoli* in soils amended with many readily available carbon sources. The increase was more pronounced when nitrogen compounds were added with organic substances; NH_4+ was much more effective than NO_3-. However, in the case of *T. basicola,* both forms of N enhanced survival of endoconidia in soil (49).

The effects of source and quantity of N on incidence of *Verticillium* wilt of cotton were studied by Ranney (58). The disease was about 50% less severe when N was provided as NH_4NO_3 rather than NH_4+ or NO_3- separately. His results require further work in order to establish cause and effect.

The utilization of inorganic N as a factor in the germination and saprophytic activity of *Fusarium roseum* Lk. (emend. Snyd. & Hans.) f. sp. *cerealis* (Cke.) Snyd. & Hans. and *F. solani* f. sp. *phaseoli* was studied by Byther (6). The germination of conidia of *F. solani* was better with NH_4+ than with NO_3-, whereas germination of *F. roseum* was not affected by N form. This relationship also generally applied for saprophytic growth of these two fungi. The author concluded that the more successful utilization of inorganic N by *F. roseum* than by *F. solani* probably contributed to its greater saprophytic ability.

According to Lu et al. (39), *Poria weirii* Murr. was not capable of utilizing NO_3-, but it did utilize NH_4+

or amino N. On the basis of this, and other information, they tentatively concluded that soil conditions that favor the presence of NO_3^- have potential in the biological control of *P. weirii* and other similar root pathogens. This is because NO_3^- is utilized by antagonistic streptomyces. Work by Whaley and Boyle (87) tends to complicate the picture. They found that some streptomyces were capable of high antibiotic production in the presence of NH_4^+, even though mycelial growth was somewhat limited.

The effect of N source on N utilization by mycorrhizal roots of beech (7) and loblolly pine (60) was recently reported. Beech mycorrhizae could absorb NH_4^+ and simple organic compounds but little or no NO_3^-. In the case of loblolly pine, NO_3^- severely reduced the formation of mycorrhizae on young seedlings.

Ritter and Lyr (62) reported on the relative efficiencies of two mycorrhizal fungi, *Suillus luteus* (L. ex Fr.) S.F.Gray and *Amanita muscaria* (L. ex Fr.) Pers. ex Hooker, in assisting Scotch pine in using various forms of P. The uptake of P was always increased with *S. luteus*, whereas with *A. muscaria*, P uptake from soluble orthophosphates was reduced and slightly above the nonmycorrhizal control plants when the P was provided as Fe-phosphate or apatite.

In the above discussion we referred to reduced inorganic N in the soil as NH_4^+. In reality, there is an equilibrium between NH_4^+ and unionized NH_3. The equilibrium is strongly pH-dependent, shifting more toward NH_3 as alkalinity increases. There is evidence that biological membranes are much less permeable to NH_4^+ than they are to NH_3. Thus, as the soil becomes more alkaline, the entry of reduced N increases, sometimes to toxic levels. This entire subject was reviewed from "onions to man" by Warren (85).

Solution effects.—The soil solution has various effects on biological activity, ranging from influences created by high salt content to dilution effects and to O_2 exclusion or transport in the soil.

Chen (9) isolated a number of osmophilic fungi from soil by the use of agar media containing 20-30% NaCl. He obtained 26 species, mostly aspergilli and penicillia. The *Aspergillus glaucus* group, particularly *Aspergillus amstelodami* (Mangin) Thom & Church, was by far the most predominant. This group is well known for its tolerance to high osmotic stresses and for its deterioration of grain in storage (10). Of the fungi isolated by Chen, only two were obligately osmophilic and one, *Scopulariopsis parvula* Morton & G.Sm., could grow in an environment saturated with NaCl. He demonstrated that most soils contain a spectrum of organisms that are capable of saprophytic activity at essentially any soil solution salt concentration. This does not indicate, however, that the microflora and microfauna are either as abundant, varied, or active in saline as in nonsaline soils.

The influence of soil salinity on the numbers and activities of the microflora was studied by Rankov (57). He found that total numbers of microorganisms were lower in saline soils (solonetz and solonchak) than in nonsaline soils, the lowest numbers being found during summer and autumn dry periods. A positive correlation between the salt content of the soil solution and numbers of microorganisms was observed up to a salt content of 0.5%. An inverse correlation was observed as the salinity increased above this value.

Rankov (57) further observed that both ammonification and nitrification decreased as salinization increased. Particular ions were found to have specific effects. The Cl-ion caused the greatest depression of both processes, sulfate significantly retarded ammonification, and carbonate depressed the development of the nitrifying bacteria.

Despite its preference for alkaline soils, *Azotobacter* did not develop well in saline soils, especially during dry periods, indicating osmotic rather than acidity difficulties (57). Cellulose decomposers and organisms that mineralize organic phosphorus compounds were also fewer in numbers in saline soils.

Rankov (57) also reported that the character, as well as the degree, of soil salinization affected the qualitative and quantitative composition of actinomycetes and fungi. *Penicillium* predominated in solonchaks and *Aspergillus* in solonetzes.

The amount of soil solution also has a definite influence on activities of the soil organisms. Many motile organisms depend on a continuous moisture film in order to move about in the soil. The salts and gases dissolved in the solution partially regulate their activities as well as the activities of nonmotile organisms.

An indication of the complexity of environmental influences on microbial activities was provided by Schneider (68) in his studies of zoospore production by *Aphanomyces cochlioides* Drechs. He found, as have others, that environmental conditions that stimulate saprophytic growth often do not stimulate spore production and release. He not only reported a definite optimum salt content (120 ppm) for zoospore production but found there was also a definite relation among the mass of vegetative hyphae, the volume of solution in which the hyphae were producing zoospores, and the numbers of zoospores produced. These studies were conducted in vitro, but they undoubtedly have important implications in host infections in soil. The fact that a pathogen, which depends on free-swimming zoospores for host infection, has evolved in such a manner that a sudden drop in osmotic tension induces the production of zoospores is quite logical. A heavy rain will both dilute the soil solution and provide the free water in the soil needed for maximum movement of zoospores through the soil to a susceptible host.

ORGANIC FACTORS.—It is not within the scope of this paper to review all effects of organic chemicals, especially pesticides, on soil organisms. Rather, the authors have selected a few specific examples to illustrate both the work that has been done and to indicate potential areas for future research.

Metabolites.—Metabolic products of soil organisms and roots are released into the soil environment, through both passive and active mechanisms, where they may exert either beneficial or detrimental effects on the activities of other organisms.

Sterols of fungal, plant, and animal origin induced sexual reproduction in species of *Pythium* and *Phytoph-*

thora and formation of large zoosporangia in *Phytophthora parasitica* Dast. var. *nicotianae* (B. de Haan) Tucker (27). Some sterols, especially cholesterol, also accelerated vegetative growth. These compounds increased the temperature tolerance in species of *Pythium* (25). Survival at both high and low temperatures was increased in the presence (in vitro) of sterols.

Certain metabolites induce an attracting (chemotactic) response by motile organisms. Rai and Strobel (56) fractionated root exudates of sugar beets to determine which portions were responsible for attraction of *Aphanomyces cochlioides* zoospores. The mixed constituents resulted in the greatest over-all response. This can be understood, since the amino acids stimulated zoospore germination and germ tube growth but did not attract zoospores. Organic acids (especially gluconic) and neutral fractions (especially glucose and fructose) attracted zoospores but did not influence their germination or development.

A very interesting chemotactic response of bacteria was demonstrated by Adler (1). Although his system was highly artificial, it could be considered as an analogue of a soil environment. Adler placed galactose and O_2 in a capillary tube (analogue of soil pores), introduced *Escherichia coli* inoculum at one end, and then sealed both ends. The *E. coli* migrated down the tube in one or two bands. If the energy source was present in excess of the O_2, the first band consumed the O_2 while using only a portion of the energy source. The second band of *E. coli* still migrated in response to a concentration gradient of the energy source but used it anaerobically. If the O_2 was present in excess of the energy source, the first wave used all the exogenous energy source aerobically, and the second wave used endogenous energy while migrating along the O_2 concentration gradient. Adler stated that "chemotaxis allows bacteria to find that environment which supplies them with the greatest supply of energy. It is clearly an advantage for bacteria to carry out chemotaxis since by this means they can avoid unfavorable conditions and seek optimum surroundings."

Certain metabolites have detrimental effects on soil organisms. Old (47) demonstrated a mycostatic effect of certain soil bacteria on the initiation of growth of spores and hyphal fragments of several soil-borne, root-rotting fungi. The effect was stronger on spores than on hyphal fragments. In culture, the bacteria produced diffusable mycostatic metabolites, which were adsorbed by charcoal, sterile soil, or exchange resins. The bacteria were found aggregated around spore germ tubes but not around inactive spores or hyphal fragments.

The above work on mycostasis illustrates a whole field of investigation which currently is receiving much attention. It illustrates that the mycostatic factor(s) is probably some form of biological metabolite. However, in calcareous soils, Dobbs and Gash (16) reported a second form of mycostasis ("residual mycostasis"), which may be mineralogical rather than biological in origin. This field offers many opportunities for contributions fundamental to our knowledge of soil chemical factors and biological activity.

Possibly the most interesting example of the influence of volatile material in the soil on biological activity has been provided by Timonin (80). He reported that a highly toxic, but selective, volatile substance is released in the soil by the insect *Scaptocoris talpa* Champ. He determined that 75 insects/banana plant, or 15-20 insects/tomato seedling, gave protection from *Fusarium oxysporum* Schlect. f. sp. *cubense* (E.F.Sm.) Wr. and *F. oxysporum* f. sp. *lycopersici* (Sacc.) Snyd. & Hans., respectively. This host plant-insect-pathogen interaction suggests numerous other possible multiple biological interactions that may occur in the soil. This area of inquiry merits considerable attention.

Other, more definable, metabolites of certain organisms appear to be important in the ecology of the soil and rhizosphere microflora. Whaley and Boyle (87) isolated several *Streptomyces* species from the rhizosphere of desert plants. These produced either heptaene or cyclohexamide antibiotics that were antagonistic to species of *Fusarium, Phymatotrichum, Rhizoctonia,* and *Verticillium*. The authors reported that the production of the antibiotics varied with the available C and N sources and that vegetative growth and antibiotic production were not necessarily correlated. For example, ammonium tartrate resulted in sparse growth but excellent antibiotic production. They concluded that "Production and excretion of heptaene antibiotics in the rhizosphere might, therefore, be possible even though an organism encounters substrates unfavorable for mycelial growth."

Marx (40) and Marx and Davey (41) reported that both physical and chemical protection of roots of shortleaf pine (*Pinus echinata* Mill.) from infection by *Phytophthora cinnamomi* Rands is afforded by the mycorrhizal condition. The mycorrhizal fungus *Leucopaxillus cerealis* (Lasch) Sing. produced the antibiotic diatretyne nitrile in vivo in quantities sufficient to give complete protection from infection by the pathogen.

A most interesting influence of metabolites on nematode activity has been reported by Hollis and Rodriguez-Kabana (29). In a rice soil, flooding in the presence of large amounts of decomposable organic matter resulted in the growth of large numbers of anaerobic, spore-forming bacteria and the production of nematocidal concentrations of *n*-butyric acid and lesser amounts of propionic acid. These acids, at the concentrations produced in the soil, killed 100% of the nematodes in a few hours. The production of toxic levels of H_2S under similar conditions was also reported (65).

As organic residues decompose in the soil, O_2 is consumed and CO_2 is liberated. Stotzky and Goos (77) reported adaptation by certain soil organisms to high levels of CO_2 and low levels of O_2, whereas other organisms did not adapt. The authors indicated the possible ecological implications of the capacity of soil organisms to adapt to adverse atmospheric conditions.

Organic amendments.—As noted above in the work of Hollis and Rodriguez-Kabana (29), the amount of decomposable organic matter in the soil influences the amount of detrimental or stimulatory chemicals released into the soil environment. In turn, the kind of decomposable organic matter also influences the types of chemicals released. Man, often accidentally but occasionally by intent, incorporates organic residues into the soil that have specific effects on biological activity. The saprophytic microflora and microfauna of the soil, when attacking fresh organic residues, may produce or release toxic compounds into the soil environment. Such toxic decomposition products have been shown to influence biological activity, root growth and plant development, and pathogenesis (3, 11, 48, 51, 54). Patrick and Koch (52) concluded that toxic decomposition products "may constitute a significant host-conditioning factor in the development of root diseases."

Some work on specific compounds released during organic residue decomposition in soil has been reported. Knösel (34) found that *p*-oxybenzoic acid was liberated by decomposing plant residues. He found that this compound had a selective action on the soil microflora, reducing the number of actinomycetes and bacteria while having no apparent effect on the soil fungi.

Soulides (74) reported that the production and stability of streptomycin and tetracycline antibiotics in soil were affected by decomposing amendments and soil mineralogy. Streptomycin was produced only in inoculated, sterilized, kaolinitic soil that was amended with soybean tissue, whereas the tetracyclines were produced in amended kaolinitic or montmorillonitic soil, whether sterilized or not.

Other decomposition products have been found that have very selective action on nematodes (53). Soluble products in soil from decomposing rye tissue were nematocidal on plant-parasitic nematodes at approximately one-tenth the concentration of that on saprophagous nematodes. The active constituent was identified as butyric acid (67).

Smith and Burns (72) showed that the soil is not homogeneous and that effects vary within both space and time in soil. They studied the microsite influence of decomposing leguminous plant tissue on nitrification in soil and reported a strong ion gradient. Ammonium was found close to the organic residue. This was surrounded by a toxic zone containing nitrite, and this, in turn, was surrounded by a zone that contained high levels of nitrate. The authors felt that such changes have important effects on the availability of plant nutrients as well as on the growth of microorganisms.

Tribe (82) studied the fate of nitrate in soil amended with cellulose film. He found that nitrate was at first taken up by the cellulolytic fungi and bacteria and kept out of solution for 5-7 weeks. At the end of that period, two-thirds to three-fourths of the cellulose was decomposed, and nitrate was again released into the soil. Tribe felt that two processes contributed to the release: (i) autolysis of microbial cells and (ii) nitrogenous excretion by the soil microfauna, which were by then active on the cellulose film. He further noted that nitrogen excretion by the soil microfauna usually is not considered in nitrogen-transformation work. However, it does occur regularly, and the nitrogen is usually in a fairly simple form (e.g., ammonium, urea, guanine, and simple proteins).

CONCLUSIONS.—In this brief review, we have attempted to demonstrate the uniqueness of the soil as a habitat for organisms and how the peculiarities of the soil chemical environment may affect, either positively or negatively, the various functions of the soil flora and fauna. Also, we have attempted the synthesis of existing information into a somewhat coherent picture and have indicated those subject areas that appear particularly promising for investigation.

Available information on the effects of soil water and clay minerals on biological processes indicates many possible, interesting interactions. Water varies in structure both within the liquid phase and in association with soil colloids, and these structural changes have important biological significance. The clay minerals partially regulate chemical processes through adsorption phenomena, thereby affecting the soil microflora and microfauna, probably to a greater extent than is now recognized. The nature of the effects of colloids will vary with the amount and type of clay minerals present.

Acidity is one of the most intensively studied of the soil chemical characteristics. It is known to alter the general nature of the soil and rhizosphere microflora, interact with nutrients in reversing mycostasis, and affect saprophytic and parasitic activities differentially. In view of the small amount of work done on the differential effects of acidity on saprophytic ability and pathogenesis, and on the potential significance of these differences, it is apparent that this field is far from exhausted. Similarly, the amounts of inorganic nutrients, and especially the different forms of the same element, may bring about noteworthy changes in parasitic activity, growth, and germination of resting stages of microorganisms. This subject is still relatively unexplored. With regard to elemental forms, more attention is surely needed to clarify the role of the saprophytic fauna in mineral transformations.

In addition to the major nutrients, several trace elements and Al, one of the most abundant elements in the soil system, may alter the general nature of the microflora and directly or indirectly affect parasitic activity.

Microbial metabolites and organic amendments also may initiate a variety of responses in the soil organisms. Some of these materials may be responsible for chemotaxis, mycostasis, toxicity, and regulation of germination and reproduction. Most of the biological interactions that take place in the soil are mediated through these metabolites. Virtually no information is available on the metabolites and excretion products of the soil fauna, although a cursory examination of the soil, especially the forest floor, frequently reveals a very large amount of these products.

It is apparent that the soil chemical environment is complex in nature and has diverse effects on biological activity within the soil ecosystem.

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